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ABSTRACT

This paper provides a descriptive overview of research on the consequences of overcrowding and the development of high population densities in animals, and speculates on the relevance of these studies for similar human phenomena. Three major foci are distinguished: (1) the effect of high population densities on animal behavior; (2) the nature of population growth in freely-growing populations confined to limited areas; and (3) the effect of high population densities on the physiological condition of animals. Effects on behavior included vicious aggression, "pansexuality," disruption of adequate maternal care behavior and withdrawal from social interaction. Where population grew freely in confined areas, populations peaked and declined and reproductive and/or maternal qualities were inhibited. Finally, there were definite physiological responses to overcrowding. It is suggested that animal studies suggest relationships we can look for in humans. (TL)

Overcrowding and Population Growth:

the Nature and Relevance of Animal Studies

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The purpose of this paper is to provide a descriptive overview of research on the consequences of overcrowding and the development of high population densities in animals, and to speculate upon the nature and degree of relevance that these studies may have for overcrowding and population growth in humans.[1]

There appear to be at least three distinguishable major foci for experimental studies in this area: 1) the effect of high population densities on the behavior of animals (i.e., do animals behave in "pathological ways" when they live in dense populations?); 2) the nature of population growth in freely-growing population confined to a limited area (i.e., do animal populations stop growing short of using up their food, water and air?) and 3) the effect of high population densities on the physiological condition of the animals (i.e., do animals living in high population densities have enlarged adrenal glands, high blood pressure, underdeveloped testes, etc.?).

All of these questions are of course very closely related and often information relative to all three may be obtained in a single study. Most studies in the area, however, can be classified as primarily oriented toward one of these three questions. Furthermore, it will be useful for our understanding to discuss results in terms of this analysis, then proceed to a suggested synthesis.

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[1]The studies in this review all deal with laboratory populations. Field studies present problems of interpretation which are beyond the scope of this paper. Discussion of field studies can be found in the reviews by Christian (1963) and Snyder (1968).

Behavioral Pathology

The production of behavioral pathology as a result of high population density is best typified by the Calhoun's (1962 a, b) studies of rat population. In fact, Calhoun's studies are the most widely known in the area in terms of being quoted by a broad range of behavioral scientists, and they provide a natural descriptive and conceptual base to begin with. Calhoun established 6 colonies of albino rats, each in an 11X14 foot room. Each room was divided into 4 pens with interconnecting ramps from pen A to B, B to C, and C to D, establishing a "straight line connection" between them. In each pen was an elevated multi-compartment high-rise nest box unit, and a food and water supply. Populations were initiated with 8 rats to a pen (4 male and 4 female), 32 to a room. The rats were allowed to live in the pens with food, water, and nesting material available for 18 months. The population was not allowed to grow unchecked. Once any room hit a level of 80 adults, succeeding generations were removed from the pens once they survived past the age of weaning. Only those animals required to make up for adult losses were allowed to survive. Calhoun removed animals and prevented the populations from skyrocketing because his aim was to observe the social reaction of rats in what he considered would be (based on 3 years of prior field study of wild rats) moderate levels of population stress. However, what he found was a severe degree of pathology developing in the animals as they continued to live under the experimental conditions. These pathological effects included an increase in physical aggression producing severe tail wounds and deep gashes in the body wall, a breakdown in maternal care behavior with an overall infant mortality rate of 96% in his first 3 rooms and 80% in the other; the development of groups

of male "prober" animals who cannibalized young and who attempted to mate indiscriminately (and inconsiderately) with females, males and juveniles; the development of "withdrawn animals" or sleepwalkers (males and females who never interacted socially); and the occurrence of intermittent, unprovoked attacks by dominant male animals upon whoever happened to be around. Calhoun characterized this situation as "social breakdown" with different groups of animals adopting different forms of pathological behavior. These effects began to develop after the population had been growing for approximately 8 months and continued to get more severe from then until the study was terminated 10 months later. The later an animal was born into the population, once the deterioration had begun, the more it showed pathology. Most of the animals born during the latter phases did not survive; those who did were in bad shape.

In discussing his results, Calhoun notes that the animals did not do anything like space themselves out evenly in the environment. Dominant animals in the end pens were able to successfully defend their territories, reducing the population pressure in their area but greatly increasing it in the middle pens. Further, a form of pathological togetherness, a "behavioral sink" developed around the feeders in the middle pens, wherein animals would congregate in large masses in order to eat together. Thus, Calhoun believes that a large part of the pathology stemmed from the animals' own social tendencies. He postulates the notion of social refractoriness in order to account for some of these results. Essentially, since there are so many animals in the same area, animals are usually interacting with an animal that has just had an interaction and therefore socially refractory; interacting with a refractory animal is unsatisfying

and at the same time produces a refractory state so that a period of time must pass before the animal will be fully responsive and able to have a satisfying interaction. However, since his social need is unsatisfied, this is a "false" refractory state and the animal keeps on interacting more and enjoying it less. An unsatisfactory copulation for a human male is a good analogy for this -- the need for sexual satisfaction is still there but the ability to satisfy it won't be present again for a while. Choosing the wrong item on a menu in a restaraunt is another analogy. Having eaten the fish, which really wasn't what you wanted, you are unsatisfied but no longer hungry so that you can't eat steak anyway. Having a two hour talk with the wrong person leaves you still wanting to talk but too tired to engage in stimulating conversation at the time, etc. So the false refractory period leaves you unsatisfied but incapable of doing anything about it for a while. As frequency of social interaction goes up past a certain point in animal populations, probability of encountering an animal in the refractory state goes up, therefore, probability of getting into a false refractory state increases. At extreme levels animals are continually interacting and continually remaining unsatisfied.

Although Calhoun's experiments remain unique as to the precise method and results, experiments on mice (Brown, 1953; Southwick, 1955; Lloyd & Christian; 1969; Snyder, 1968) and on voles (Clarke, 1955) have noted a similar pattern of pathological effects: increased aggression and physical damage; breakdown in maternal care; high infant mortality and social disorganization with different sub-groups of animals responding in different ways. It should be noted that these severe effects have been obtained in breeding populations in relatively large but confined spaces and over a relatively long time period (a year or more).

Population Growth in Confined Space

The second focus of investigation, nature of population growth in confined populations, stems from at least as far back as the work of Crew and Miraskala, in 1931, who noted the decline in reproductive success in mice maintained in a confined area. We shall discuss an experiment by Southwick (1955) as a representative of this class.

Southwick raised 6 populations of house mice in pens, 6' X 25'. Each population was formed from 4 pairs of healthy young adult feral house mice. He supplied each pen with 48 nest boxes and with ad lib food, water and nesting material daily. In 3 of the pens, nest boxes as well as food and water supplies were distributed evenly over the area; in the other 3 nest boxes were concentrated at one end of the pen and food and water were concentrated at the other. After maintaining his populations for 2 years, Southwick noted that they all peaked and declined, and that the major proximate cause of this decline was the failure of the young to survive. The peak size attained by the different populations ranged from 25 to 138. The concentrated versus spaced nest box and food conditions did not appear to have an effect. Southwick notes that the history of each population was different and that the different population sizes attained are due to "intrinsic fadtors" in each population "...differences in the social behavior of the populations apparently account for the variability in population growth." He notes that actual pregnancy rates and birth rates declined in some of the pens, as well as the high rate of infant mortality which was common to all of them. Southwick noted that population decline was correlated with what he termed "internal strive" in the populations,

(e.g., this essentially refers to the syndrome described by Calhoun: intensive aggressive activity, breakdown of female nest defense, disruption of nest building, and "general social instability" leading to cannibalism and litter desertion). Southwick essentially treats these responses as a behavioral criterion of crowding, but notes that this "crowding" is not a simple response to number of animals per square foot. In his words, "I conclude that these behavioral traits were related to crowding and confinement, but not to density per se for the population of pen E was crowded at a density of 1 per 10 square feet whereas other pens were not crowded until they reached densities ten times greater."

A variety of other studies, primarily with mice, have confirmed Southwick's basic findings that confined populations are usually self-limiting, (that is, population growth stops before available space, food and water is fully utilized) and that there is wide variation in the maximum population size attained under identical physical conditions. Terman (1965) has added an important observation that relates reproductive success to social structure. At high population densities, most female deermice in his population simply did not reproduce, but the dominant females continued to have litters as before. Hence, for reproduction as for behavioral pathology, the effects are not evenly distributed throughout the population.

Beyond the fact the population numbers reach an asymptote and decline, the long term fate of confined populations is usually not determined. In some populations (Calhoun, 1962; Southwick, 1955) the process appears to be one that eventually leads to extinction of the population. Snyder (1968), however, ran a 3 year study of a confined moose population and found indications of cyclic process. The population rose to almost 200 animals in the first 12 months, declined sharply over the next year to below 50, then began to increase again and rise to 150 when a new decline set in and the experiment was terminated.

It is clear that the major factor in population decline in most studies has been failure of the young to survive to the age of weaning. Litters continue to be produced, but the infants die. However, there are other effects of crowding on the reproductive process that may contribute to the self-regualtion of confined populations. These include an increase in intra-uterine mortality (Christian, 1956; Christian & LeMunyan, 1958), shortening or elimination of the estrous cycle (Whitten & Simply, 1959) and failure to become pregnant either because of infertility or because of failure to engage in reproductive activity (Terman, 1965).

Physiological Responses to Overcrowding

The pattern of physiological responses to overcrowding are essentially those described as the chronic stress response or general adaptation syndrome by Selye (1946). The stress response as a short term condition mobilizes the energies of the body for emergency reactions. (The pattern of response is characterized physiologically by activities such as, marked adrenal gland activity, (secretion of ACTH from the adrenal cortex as well as epinpherine and nor-epinepherine from the adrenal medulla), release of glycogen from the liver into the blood stream suppression of digestive activity, increase in antibodies in the blood, etc. As a long term or chronic response, the stress reaction tends to deplete some of the bodies resources and lead to degenerative changes in parts of the endocrine system. (These include suppression of pituitary gonadotropic activity, atrophy of the thymus gland, and degeneration of lymph nodes with attendant reduction of antibody production). Many experimental investigations have been concerned with looking for one or more of the symptoms of chronic stress in animals raised under different social conditions. (Reviews of the literature include those of Thiessen, 1961 and Christian, 1965). The most frequent

measure utilized is size of the adrenal gland; chronic activity leads to enlargement of this structure. Measurement techniques range from the crude weighing of adrenals (for which body size, nutrition and other factors have to be taken into account) to histological examination of adrenal cell structure for evidence of chronic activity.

Other measures taken to reflect (directly or indirectly) a chronic stress reaction include increased cortico-steroid levels of blood or urine, decreased size of gonads, decreased antibody response, and atrophy of the thymus gland (Mason, 1959; Pruduvsky, 1959). The studies cited above all find evidence that animals housed in groups show evidence of the particular symptom associated with stress. Again, the majority of the studies use small rodents as subjects. Several studies provide interesting insights as to the psychological basis of these effects. Christian (1955) found enlarged adrenals in albino mice in groups of 4, 5, or 6 as opposed to isloated controls. In some of his groups there was much fighting and the presence of scar tissue reflecting actual wounding. In some there was no fighting. However, he gound no correlation between adrenal size and presence or absence of fighting or degree of fighting or scarring. He concludes that it is not fighting per se that induces the changes but "sociopsychologic pressures" alone.

In another study, Davis & Christian (1957) found that in groups of 6 mice where there was clearly a dominant animal the adrenals were enlarged in the subordinate animals but not in the dominant one. Christian suggests that essentially any encounter between a dominant and subordinant animal may be stressful for the latter but not at all for the former. (i.e., while the dominant animal is out for a relaxed evening stroll the adrenal glands of the subordinates he encounters along the way are pupping like mad.)

Finally, a recent study on resistance to infection as related to fighting raises some fascinating questions about the relationship between stress and disease in populations as well as being a nice illustration of the differences in effects between acute and chronic stress. Jackson and Farmer (1970) infected male mice with Nsoma and studied the course of the infection. A control group of animals lived alone during the entire experiment. A second group had been housed in pairs under conditions that elicited considerable fighting for a period of 10 days prior to being infected, then were housed in isolation. A third group was housed alone prior to infection then fought for 10 days afterward. It was found that after 10 days infection levels were higher in mice who had fought prior to infection and lower in those who fought after infection. These results can be understood if we look at the effects of a single injection of ACTH and cortisone on antibody response as compared to repeated injections over a long period of time. After a single dose, antibody levels in the blood rise but after 24 hours return to normal. With repeated injections antibody response is lowered. Thus, animals who have fought for 10 days prior to infection have a lowered capability to produce antibodies and fight the infection. Animals who fight only after infection still have the capability for an immediate elevated antibody response upon the initiation of fighting. This markedly inhibits the growth of the disease immediately.

It is clear that these 3 major foci are intimately related. In confined populations it may be stated simply that overcrowding produces behavioral disorganization and physiological changes which combine to interfere with reproduction and survival of young, thereby limiting population growth.

Summary and Conclusions

I. Categorization of 3 Major Focii of Animal Studies

A.) Effect of density on behavior

B.) Population growth and decline of defined space

C.) Effect of density on physiology

II. Discussion of Each of These

A.) "Reference" study is by Calhoun. Raised rats in 11 X 14' rooms. Let populations grow to 80 per room -- removed excess animals beyond that point. Found extreme behavioral pathology.

1. Vicious aggression, unprovoked and unsignalled.
2. "Pansexuality" -- loss of discrimination of appropriate cues for mating -- males would attempt to mate with females whether or not they were receptive, with other males, and even with juveniles.
3. Disruption of adequate maternal care behavior.
4. Withdrawal from all social interaction -- animals that move like "sleepwalkers" through the population.

Several other studies of rodents generally confirm Calhoun's findings. Calhoun notes that animals did not exploit the physical environment equally and that much of the pathology was a result of their own gregarious tendencies, which can result in the formation of a "behavioral sink", an area which pulls in a large number of animals. He notes that males who defended territory successfully and females who lived within defended areas showed less evidence of pathology. In discussing the broad implications of his results, Calhoun proposes the concept of social refractoriness.

Calhoun postulates that animals have a number of specific social needs. If A interacts socially with B, then the social need is satisfied and both A and B are now in a refractory state for a period of time with respect to some types of social interaction. If C now comes along and interacts with A, a "false refractory" period will be set up in C. As a result of interacting with A, C will be refractory for further social interaction of that type but since A was refractory and in some ways inattentive, C will still be unsatisfied. Thus, C is unsatisfied and also not able to achieve satisfaction until the refractory period wears off.

8.) Studies of growth in confined experimental populations go back at least as far as 1931. Southwick's (1955) study is representative. He raised 6 populations of house mice; ½ under "massed housing" conditions (all nest boxes at one end of pen, food and water in 2 large bowls) and the other under spaced conditions (nest boxes spread out over entire pen, food and water in 24 different bowls.) Found that despite the fact that there was always plenty of food and water and surplus nesting space, populations stopped growing. Great variability in size -- they ranged from 25 to 138. Each population had somewhat of its own unique history. The point of behavioral crowding differed according to the types of social structure that developed --massed vs. spaced conditions had no effect.

Other studies have confirmed that 1) population of rodents usually peak and decline well before physical resources are depleted; 2) variability in population size in the same physical space is rule; 3) the population growth is inhibited by the failure of infants to survive and a reduction in birth rate. In any case, reproductive and/or maternal qualities appear to be totally inhibited.

C.) Physiological response to overcrowding follows that classic stress or "general adaptation syndrome" described by Selye. This includes enlarged adrenal glands, reduced glycogen storage in the liver, degeneration of lymph nodes (increasing susceptivility to infection), decreased growth rate, decreased gonadal functioning. These changes occur often simply through "enforced social contact"; aggression or fighting is not necessary to produce these changes. Where there is aggression or fighting, dominant animals show much less of a physiological stress response than do subordinate animals.

It is clear that these 3 major foci are intimately related. It may be stated simply that overcrowding produces behavioral disorganization changes which combine to interfere with reproduction and durvival of young, thereby limiting population growth.

III. Conclusions and Hypotheses

Experimental animal studies thus far have been limited largely to small rodents and this perforce limits our perspectives. We need a much broader comparative base. There are 2 types of information to be gained from these studies that have relevance to humans. One is to gain perspective -- animal studies suggest relationships that we can look for in humans -- this does not imply any necessity that the relationships found in anirals will be obtained in humans. The second is the specific data on physiological changes, which is very likely to be rather directly generalizable to humans, given the fact that the stress response appears phylogenetically very old and common to all mammals.

The conclusions to be drawn from physiology are clear enough. Large segments of the human population may be suffering from the "stress response" syndrome without necessarily being aware of high levels of psychological stress at any one time. This has many ramifications which are in need of research. One practical notion is that physiological measures (such as corticosteroids in urine) be utilized to determine average stress levels in different kind of housing arrangements.

Some perspectives that can be drawn from animal studies thus far are:

A) "Crowding" is in large part a social phenomenon in that the same physical space may or may not be crowded depending on how it is utilized for social interactions.

B) The effect of overcrowding can be very different as diffenent individuals in the population -- individuals with high social rank will be less affected than lower ranked individuals. This is true for all of the effects noted -- behavioral, "pathology", reproduction, and stress responses. Further, different modes of behavioral adaptation may occur. Extreme aggressiveness and hyperactivity at one end and behavioral sleepwalking at the other.

C) Effects of overcrowding are more profound on individuals who are born into an overcrowded population than on those who were raised in "better times" and had to deal with overcrowding as adults.

D) The inhibition of population growth with overcrowding is not an automatic "triggering" of some self-regulating impulse, but the net result of a number of behavioral and physiological changes the result from overcrowding.

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